

# NOTES ON THE COURTSHIP BEHAVIOR OF *APLASTODISCUS ARILDAE* (CRUZ & PEIXOTO, 1985) AT AN URBAN FOREST FRAGMENT IN SOUTHEASTERN BRAZIL (AMPHIBIA, ANURA, HYLIDAE) <sup>1</sup>

(With 2 figures)

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ABSTRACT: The courtship behavior, advertisement call, and courtship call of *Aplastodiscus arildae* are described based on observations realized at Parque das Mangabeiras, Belo Horizonte, Minas Gerais, Southeastern Brazil. Calling males were observed at leaves above the stream or on the litter near rivulet banks approximately all year. Female is attracted by the calling male and conducted to the subterranean nest, a different place from the calling site. The courtship event involves alternated mutual touches by the couple and calls with higher repetition rate emitted by the male. *Aplastodiscus arildae* presents reproductive mode with aquatic eggs deposited in subterranean nests. The advertisement call and courtship call consisted of a sequence of a unique no pulsed note, but the first presents larger interval among the calls and duration and higher dominant frequency than the last.

Key words: Hylidae. Aplastodiscus arildae. Courtship behavior. Courtship call. Advertisement call.

RESUMO: Notas sobre o comportamento de corte de *Aplastodiscus arildae* (Cruz & Peixoto, 1985) em um fragmento florestal urbano no sudeste do Brasil (Amphibia, Anura, Hylidae).

O comportamento de corte e os cantos de anúncio e de corte de *Aplastodiscus arildae* são descritos com base em observações realizadas no Parque das Mangabeiras, Belo Horizonte, Minas Gerais, Sudeste do Brasil. Machos vocalizam praticamente por todo o ano, utilizando como sítios de vocalização a vegetação marginal ou o folhedo no barranco na margem de riachos. A fêmea é atraída pelo macho vocalizante, que a leva até o ninho (uma toca subterrânea), que se situa em local diferente do sítio de vocalização. No processo de condução ao ninho estão envolvidos toques mútuos entre os indivíduos e emissões de canto de corte emitidas pelo macho. *Aplastodiscus arildae* apresenta modo reprodutivo com ovos aquáticos depositados em ninhos subterrâneos. Os cantos de anúncio e de corte consistem de seqüências de uma única nota não pulsionada, sendo que o primeiro apresenta maior intervalo entre cantos e duração e freqüência dominante mais elevada que o segundo.

Palavras-chave: Hylidae. Aplastodiscus arildae. Comportamento de corte. Canto de anúncio.

## INTRODUCTION

Courtship behavior refers to interactions between males and females to evaluate each other before the pair formation and mating, including the use of signals by courting males (Wells, 1977). Courtship in frogs involves basically production of advertisement calls by males (Duellman & Trueb, 1986). However, literature describing more complex signals on courtship of frogs has been increasing (e.g. Haddad & Sawaya, 2000; Lima et al.,

2002; Lima & Keller, 2003; Hartmann *et al.*, 2004). Reproductive modes in amphibians are a combination of ovipositional site, ovum and clutch characteristics, rate and duration of development, stage, and size of hatchlings and type of parental care, if any (Salthe, 1969; Salthe & Duellman, 1973). The greatest variability of reproductive modes in amphibians is known for the neotropical species (Duellman, 1985; Hödl, 1990) and anurans show more diversity of trends than other amphibians (39 distinct reproductive modes) (Haddad & Prado, 2005).

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The family Hylidae is one of most diverse families among anurans, with more than 800 species (FAIVOVICH et al., 2005), and a broad distribution in Brazil. Haddad & Prado (2005) recognized 11 reproductive modes to this family. The green treefrogs of genus Aplastodiscus presents an apparent synapomorphy related to the reproductive mode, where male constructs a subterranean nest in the muddy side streams or ponds. This genus included three species group. One of them, Aplastodiscus albofrenatus group, contents the following species: A. albofrenatus (A.Lutz, 1924); A. arildae (Cruz and Peixoto, 1985); A. ehrhardti (Müller, 1924); A. eugenioi (Carvalhoe-Silva and Carvalho-e-Silva, 2005); A. musicus (B.Lutz, 1948); and A. weygoldti (Cruz and Peixoto, 1985) (FAIVOVICH et al., 2002; 2005). The species of A. albofrenatus group are distributed within the Atlantic Forest domain, from Santa Teresa, State of Espírito Santo, to São Bento do Sul, State of Santa Catarina, Brazil (CRUZ & PEIXOTO, 1985).

Natural history of these green treefrogs species are nearly unknown, with the exception of *A. leucopygius* (Haddad & Sawaya, 2000), *Aplastodiscus* sp. (aff. *ehrhardti*) (Hartmann *et al.*, 2004), and anecdotal information for some species as *A. albofrenatus* (Hartmann *et al.*, 2004) and *A. eugenioi* (Carvalho-e-Silva & Carvalho-e-Silva, 2005).

Aplastodiscus arildae is registered at Serra do Mar, Serra da Mantiqueira, and Serra do Espinhaço mountain ranges located in the southeastern Brazilian region (Pedralli et al., 2001; Frost, 2004; Nascimento et al., 2005). The knowledge of natural history of A. arildae is scarce. Cruz & Peixoto (1985) reported the habitat use for this species and Haddad & Sazima (1992) present anedoctal informations. Herein, we describe the advertisement call, courtship call, and provide observations of courtship behavior of A. arildae from a secondary forest fragment in Minas Gerais, Brazil.

### MATERIAL AND METHODS

Observations were made during May 2000 to December 2001, November and December 2002 at Parque das Mangabeiras, an urban forest fragment of Belo Horizonte, Minas Gerais, southeastern Brazil (19°55'57"S - 43°56'32"W, at 800-1000m). This fragment is located in the Serra do Curral, a small mountain range belonging to the Espinhaço Mountain Complex, in a transitional region between Atlantic Forest and Cerrado domains (sensu AB'SABER, 1977).

We observed the courtship behavior of *A. arildae* from 20:50h to 23:50h on 22 October 2001 and from 20:30h to 21:30h on 23 December 2002. The times described in the text are presented by the interval 00' to 180'. Focal-animal and all-occurrence samples were used in both observations (Lehner, 1979), which were made by a flashlight with a red filter to reduce the light interference on the behavior of the treefrogs. In order to stimulate males we played playback with advertsiment calls to resident males. The playback was previously recorded using a portable tape recorder Panasonic RQ-L309.

We recorded the advertisement and courtship calls with a TASCAM DAP1 recorder and Sennheiser M66 microphone from a male on 2 November 2002. The sonograms were produced by PC computer coupled to the software Avisoft-Sonagraph Light version 2.7. The oscilogram and power spectrum were obtained by PC computer coupled to the software Sound Ruler version 0.941 (Gridi-Papp, 2003-2004). Vocalizations were edited at a sampling frequency of 22 kHz, FFT with 256 points, 16-bit resolution, 50 overlap, and Flap top window.

ANOVAs and Mann Withney test were performed, to compare the calls parameters, with the software Statistica for Windows version 5.1 (STATSOFT, 1995), as according to the variance assumptions of homocedasticity and normality. To test these premises it was used Levene and Komogorov-Smirnov's tests, respectively. The significance index was established as 0.05.

#### **RESULTS**

Calling males of Aplastodiscus arildae were observed at night during all months in which observations were made, on leaves above streams, or on the litter near rivulet banks in forested areas. In 22 October 2001, two males and one female were observed at a rivulet bank, spatially distributed on the vegetation (Fig.1A). At the beginning of observation, the two males were 0.3m and 0.2m above the ground and 1.5m and 2.15m from the rivulet, respectively. The initial distance between males was 0.65m. A female was observed on the ground, 1.5m from the stream. At time 00' only male A was emitting advertisement calls on a low emission rate (not tape recorded). At time 5', we started the playback from the ground, 0.7m of male A, 0.5m of male B and 0.45m of the female, to stimulate the vocalization activity of the males. Male A answered the playback immediately and kept calling until time 10'. Then the female turned

and moved toward the playback. After touching the recorder, she promptly jumped 0.38m to the rivulet. We continued the playback and male A emitted vocalizations on a high emission rate (not tape recorded), attracting the female to him (Fig. 1B). She climbed a shrub and stopped above male A. At time 50', she jumped upon male A (Fig.1C), moved to his side, and stayed in this position for 5 minutes. At the time 55', the couple alternated mutual touches using their hands (Fig. 1D). After this sequence of touches, male A stopped calling and started moving toward the rivulet through the vegetation (Fig. 1E). When the male A was far from the female, he stopped and emitted calls with higher repetition rate, here considered as courtship calls (see Haddad, 1995), until the female approached and touched him (Fig. 1F). The couple then jumped onto a rock in the middle of the rivulet, where they alternated mutual touches again, sometimes using the side of the head (Fig.1G). This sequence was performed from 63' to 73'. The distance covered by the couple from the beginning of the observations to time 73' was 2.40m along the rivulet bank. Male B kept at the same position, sometimes emitting calls with lower intensity than courtship calls, and did not disturb the pair during the interaction.

At time 75', the couple climbed down the rock and moved 0.75m to a hollow entrance, a small slit between rocks at the edge of rivulet, at the water level. Only the male went into the hollow and the female stayed at the entrance for approximately 15 minutes (Fig.1H). At time 90', the female also went into the hole and we were unable to observe the couple further. Clutch and tadpoles were not observed, although we fenced the hollow entrance at the following morning and monitored it once a week during the following month.

During the second observation (23 December 2002), a female and three calling males were observed and the behavior of the female in choosing the male was the same as described before. However, it was possible to observe the process by which the male guided the female to the nest site in more detail. After the female reached the selected male, they exchanged touches for a few minutes. Then the male started to move through the vegetation, followed by the female. The male stopped on a branch and when the female reached him, they exchanged mutual touches. When the male jumped to another branch, he begun to emit

courtship calls with the head turned toward the female (n=2) or shook the branch, vibrating the perch of female (n=2).

The advertisement and courtship call of *Aplastodiscus arildae* are described from the male recorded on 2 November 2002, at air temperature of 23°C. The adversiment call consisted of a sequence of tonal note; the intervals between consecutive calls ranged from 0.85 to 2.83s ( $\bar{x}$ =1.38, SD=0.41, n=83); the note duration ranged from 0.053 to 0.072s ( $\bar{x}$ =0.064, SD=0.003, n=78); the dominant frequency ranged from 2763.4 to 2870.7Hz ( $\bar{x}$ =2846.8, SD=23.3, n=83) (Figs.2A, B, C).

The courtship call of *A. arildae* consisted of a sequence of tonal note; the intervals between consecutive calls ranged from 0.464 to 1.154s ( $\bar{x}$ =0.819, SD=0.156, n=66); the note duration ranged from 0.021 to 0.047s ( $\bar{x}$ =0.037, SD=0.004, n=70); the dominant frequency ranged from 2843.9 to 3004.9Hz ( $\bar{x}$ =2950.8, SD=23.95, n=70) (Figs.2D, E, F).

The advertisement call has larger calls intervals (U=357.0; p=0.0) and note duration call ( $F_{2,150}$ =1925.6, p=0.0), and higher dominant frequency ( $F_{2,150}$ =737.9, p=0.0) than courtship call.

#### DISCUSSION

Female choice in both events observed in *Aplastodiscus arildae* seems to be based partially on acoustic signals and the courtship behavior observed includes mutual touches and acoustictactile interactions. Reproductive behavior characterized by a stereotyped sequence of mutual touches between both sexes and the male guiding female to an oviposition site is characteristic of species which the male constructs a nest site (e.g. Hylodes phyllodes Heyer and Crocoft, 1986 - FARIA et al., 1993); Hylodes asper (Müller, 1924) - Haddad & Giaretta, 1999; A. leucopygius – Haddad & Sawaya, 2000; Aplastodiscus sp. (aff. ehrhardti) - Hartmann et al., 2004; A. perviridis A.Lutz, 1950 - Haddad et al., 2005). In these cases, the final selection of the partner still remains with the female, which may be also based on characteristics of the nest (see HADDAD & SAWAYA, 2000).

Hartmann *et al.* (2004) observed three stages of courtship behavior for *Aplastodiscus* sp. (aff. *ehrhardti*): (1) preliminary female choice, (2) interactive courtship, and (3) acceptance or refusal of the male and/or subterranean nest by the female.

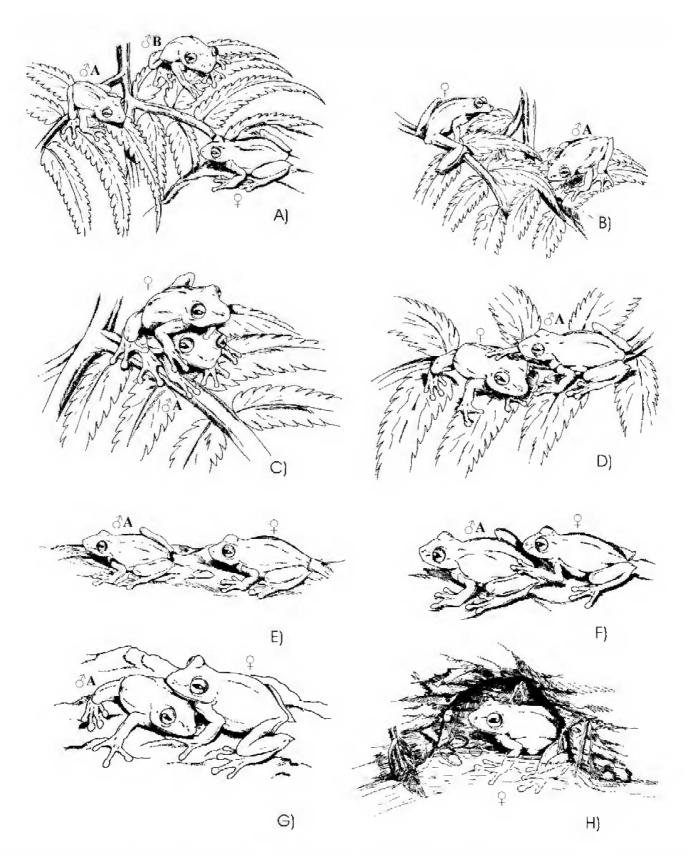


Fig.1- Schematic diagram showing the reproductive behavior of *Aplastodiscus arildae* at Parque das Mangabeiras, Belo Horizonte, Minas Gerais, Brazil: (A) individuals of *A. arildae* at the beginning of observations; (B) female closed to male A; (C) female above the male A; (D) female touching the dorsum of male; (E) male guiding the female; (F) female touching male during the trajectory; (G) mutual touches by the couple using the lateral part of heads; (H) female at the hollow entrance. Drawings based on the narrative recording during field observations and photos.

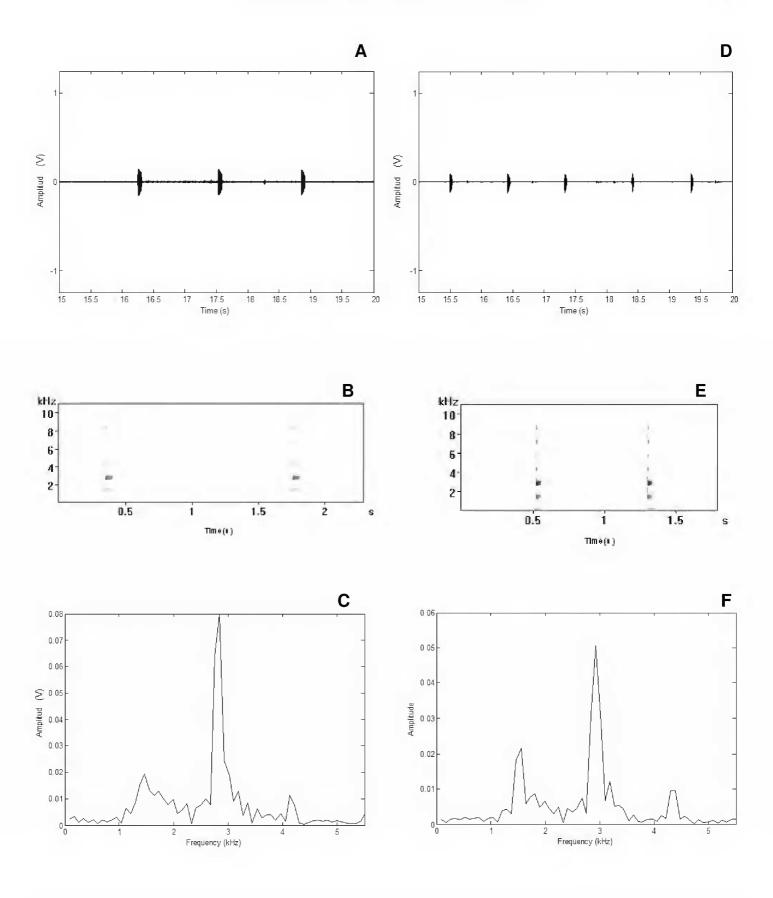


Fig.2- Advertisement call (A) oscilogram; (B) sonogram of sequence of two calls; (C) power spectrum and courtship call (D) oscilogram; (E) sonogram of sequence of two calls; (F) power spectrum of *Aplastodiscus arildae* at Parque das Mangabeiras, Belo Horizonte, Minas Gerais, Brazil (air temperature 23°C).

Although we did not observe any kind of choice related to nest characteristics for *A. arildae* female, we hypothesized that female choice relied on acoustic selection at the beginning of courtship and not at the end of the whole process. The elaborate courtship behavior observed, the long distance from vocal site to the nest, the likelihood of a predator encounter, and the risks for the female to be intercepted by a satellite males during the trajectory, could make the choice after the inspection of the nest costly for both males and females. Hence, the final selection on the basis of the nest characteristics (Haddad & Sawaya, 2000; Hartmann *et al.*, 2004) might be cautiously invoked and so more detailed studies are needed to evaluate these hypothesis.

Although the function of visual cues has only ocassionally been tested experimentally, the results suggested that visual signaling is a significant mode of communication in a few anuran species (Hödl & AMÉZQUITA, 2001). This kind of communication is better known for diurnal species (e.g., Colostethus trinitatis Garman, 1888 - Wells, 1980; Brachycephalus ephippium Spix, 1824 - Pombal et al., 1994; Hylodes asper – Haddad & Giaretta, 1999). OWASKA & RAND (2001) pointed out that Eleutherodactylus diastema Stejneger, 1904, a nocturnal species, probably uses visual cues during reproductive display, as is known for *Phyllomedusa* distincta Lutz, 1950 (Castanho, 1994). Aplastodiscus sp. (aff. ehrhardti) presents a visual signaling and a diverse repertoire of limb movements exhibited by both sexes. Male and female show a stereotyped behavior, moving the limbs up and down, alternating positions, and sometimes being face to face, sometimes side by side (HARTMANN et al., 2004). Courtship in this species has greater duration compared to other amphibians and this long interaction between males and females may have at least three purposes: (1) to evaluate the reproductive condition of the mate, because elaborate behavior may indicated physiological condition and individual attributes, influencing acceptance or refusal of the mate; (2) to stimulate ovulation, as relative long periods of courtship may be necessary to trigger ovulation; and/or (3) to lead the female from the calling site to the nest passing obstacles such as leaves, trunks, and roots that could obstruct progress to the nest (see Hartmann et al., 2004).

Inasmuch as *A. arildae* is nocturnal, we believe that the decreased moonlight reduces the probability of visual communication, based on the fact that the male emitted courtship calls and waited for the female to touch him. In contrast with *Aplastodiscus* sp. (aff.

ehrhardti), in A. arildae, as in A. leucopygius, courtship involves calls and tactile signals. Mechanical vibration of the vegetation branches could be an additional way to male conduct the female in A. arildae.

Hödl & Amezquita (2001) indicated that some special ecological conditions favored the evolution of visual signals. These ecological conditions are displaying at elevated perches, diurnality, aposematism and displaying at continuous high environment noise levels. Except by the period of activity, *Aplastodiscus arildae* at Parque das Mangabeiras are under these ecological conditions. Therefore, it is essencial to have more observations to conclude that this species do not present visual communication. In spite of insufficently observations, we suggested that *A. arildae* could present an additional way of communication, a mechanical vibration of the substrate.

Calling sites that differ from oviposition sites also are found in other tropical hylids species (e.g., *D. elegans* Wied-Neuwied, 1824 – Bastos & Haddad, 1996; *A. leucopygius* – Haddad & Sawaya, 2000; *Aplastodiscus* sp. (aff. *ehrhardti*) – Hartmann *et al.*, 2004). Haddad & Sawaya (2000) showed for *A. leucopygius* and Hartmann *et al.* (2004) for *Aplastodiscus* sp. (aff. *ehrhardti*) that call sites are on leaves under water and the oviposition site are subterranean nests. *Aplastodiscus arildae* males used leaves above the water as calling sites too. Although we did not observe the direct events of oviposition, we considered the courtship behavior described for *A. arildae* as evidence that this species deposits eggs in subterranean nests.

The reproductive behavior of A. arildae is similar to that described for A. leucopygius (see HADDAD & SAWAYA, 2000) and Aplastodiscus sp. (aff. ehrhardti) (HARTMANN et al., 2004). Thus, the reproductive mode for A. arildae consisted of: aquatic eggs; eggs and early larval stages in subterranean constructed nests; subsequent to flooding, exotrophic tadpoles in ponds or streams (mode 5, sensu Haddad & Prado, 2005). Further studies should be addressed to precisely evaluated this aspect. Therefore, the evidences of equal events on courtship behavior and reproductive mode for A. arildae, A. leucopygius (see HADDAD & SAWAYA, 2000) and Aplastodiscus sp. (aff. erhardti) (see HARTMANN et al., 2004), even though to A. perviridis (HADDAD et al., 2005) may have confirm the monophyletism of this group as suggested by Haddad et al. (2005) and proposed by Faivovich et al. (2005). The advertisement call here described presents differences for dominant frequency and interval among calls from that reported by Heyer et al.

(1990) for *A. arildae* at Boracéia, São Paulo, Brazil. The maximum frequency in their sonogram was approximately 4000Hz and the calls intervals ranged from 0.7 to 1.7s (21.8°C air temperature). The advertisement and courtship calls from the present study were recorded from the same male, at the same night, by the same air temperature, but over different behaviors. The advertisement calls was emitted at the absence of female and the courtship calls were only emitted when the male and female begun the trajectory to the oviposition site.

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# REFERENCES

AB'SÁBER, N.A., 1977. Os domínios morfoclimáticos na América do Sul. Primeira aproximação. **Geomorfologia, 52**:1-21.

BASTOS, R.P. & HADDAD, C.F.B., 1996. Breeding activity of the neotropical treefrog *Hyla elegans* (Anura, Hylidae). **Journal of Herpetology**, **30**(3):355-360.

CARVALHO-E-SILVA, A.M.P.T. & CARVALHO-E-SILVA, S.P., 2005. New species of the *Hyla albofrenata* group, from the States of Rio de Janeiro and São Paulo, Brazil (Anura, Hylidae). **Journal of Herpetology, 39**(1):73-81.

CASTANHO, L.N., 1994. História natural de *Phyllomedusa distincta*, na Mata Atlântica do Município de Sete Barras, Estado de São Paulo (Amphibia, Anura, Hylidae). 99p. Dissertação (Mestrado em Ecologia), Universidade Estadual de Campinas, Campinas.

CRUZ, C.A.G. & PEIXOTO, O.L., 1985. Espécies verdes de *Hyla*: o complexo "albofrenata" (Amphibia, Anura, Hylidae). **Arquivos da Universidade Federal Rural do Rio de Janeiro**, **7**(1-2):59-70.

DUELLMAN, W.E., 1985. Reproductive modes in anuran amphibians: phylogenetic significance of adaptive strategies. **South African Journal of Science**, **81**:174-178.

DUELLMAN, W.E. & TRUEB, L., 1986. **Biology of Amphibians**. New York: McGraw-Hill. 670p.

FAIVOVICH, J.; CRUZ, C.A.G. & PEIXOTO, O.L., 2002. The identity of *Hyla ehrhardti* Muller, 1924 (Anura: Hylidae). **Journal of Herpetology**, **36**(2):325-327.

FAIVOVICH, J.; HADDAD, C.F.B.; GARCIA, P.C.A.; FROST, D.R.; CAMPBELL, J.A. & WHEELER, W.C., 2005. Systematic review of the frog family Hylidae, with special reference to Hylinae: phylogenetic analysis and taxonomic revision. **Bulletin of the American Museum of Natural History**, **294**:1-240.

FARIA, D.M.; CASAIS SILVA, L.L. & RODRIGUES, M.T., 1993. Nota sobre reprodução de *Hylodes phyllodes* (Anura, Leptodactylidae). In: CONGRESSO LATINO AMERICANO DE HERPETOLOGIA, 3., 1993, Campinas. **Resumos...** Campinas: Universidade Estadual de Campinas. p.150.

FROST, D.R., 2004. **Amphibian Species of the World – an on line reference**. Disponível em: <a href="http://research.amnh.org/herpetology/amphibia/index.html">http://research.amnh.org/herpetology/amphibia/index.html</a>. Acesso em: 10 jun. 2005.

GRIDI-PAPP, M. 2003-2004. Sound Ruler: Acoustic Analysis, versão 0.941. Disponível em: <a href="http://soundruler.sourceforge.net/oldsite/index-br.htm">http://soundruler.sourceforge.net/oldsite/index-br.htm</a>. Acesso em: 15 jul. 2006.

HADDAD, C.F.B., 1995. Comunicação em anuros (Amphibia). In: TITTO, E.A.L.; ADES, C. & COSTA, M.J.R.P. (Orgs.) **Anais de Etologia,** XIII, 1. São Paulo: Editora Pirassununga, Sociedade Brasileira de Etologia. p.116-132.

HADDAD, C.F.B. & SAZIMA, I., 1992. Anfibios Anuros da Serra do Japi. In: MORELLATO, L.P.C. (Org.) História natural da Serra do Japi: Ecologia e preservação de uma área florestal no sudeste do Brasil. 1.ed. Campinas: UNICAMP/FAPESP. v.1, p.188-211.

HADDAD, C.F.B. & GIARETTA, A.A., 1999. Visual and acoustic communication in the Brazilian torrent frog, *Hylodes asper* (Anura: Leptodactylidae). **Herpetologica**, **55**(3):324-333.

HADDAD, C.F.B. & SAWAYA, R.J., 2000. Reproductive modes of Atlantic forest hylid frogs: a general overview with the description of a new mode. **Biotropica**, **32**(4b):862-871.

HADDAD, C.F.B. & PRADO, C.P.A., 2005. Reproductive modes in frogs and their unexpected diversity in the Atlantic forest of Brazil. **BioScience**, **55**(3):07-217.

HADDAD, C.F.B.; FAIVOVICH, J. & GARCIA, P.C.A., 2005. The specialized reproductive mode of the treefrog *Aplastodiscus perviridis* (Anura: Hylidae). **Amphibia-Reptilia**, **26**(1):87-92.

HARTMANN, M.T.; HARTMANN, P.A. & HADDAD, C.F.B., 2004. Visual signaling and reproductive biology in a nocturnal treefrog, genus *Hyla* (Anura:Hylidae). **Amphibia-Reptilia**, **25**(4):395-406.

HEYER, W.R.; RAND, A.S.; CRUZ, C.A.G.; PEIXOTO, O.L. & NELSON, C.E., 1990. Frogs of Boracéia. **Arquivos de Zoologia**, **31**(4):231-410.

HÖDL, W., 1990. Reproductive diversity in Amazonian lowland frogs. **Fortschritte der Zoologie**, **38**:41-60.

HÖDL, W. & AMÉZQUITA, A., 2001. Visual signaling in anuran amphibians. In: RYAN, M.J. (Ed.) **Anuran Communication**. Washington: Smithsonian Institution Press. p.121-141.

LEHNER, P.N., 1979. **Handbook of Ethological Methods**. New York: Garland STPM Press. 403p.

LIMA, A.P.; CALDWELL, J.P. & BIAVATI, G.M., 2002. Territorial and reproductive behaviour of an amazonian dendrobatid frog, *Colostethus caeruleodactylus*. **Copeia**, **2002**(1):44-51.

LIMA, A.P. & KELLER, C., 2003. Reproductive characteristics of *Colostethus marchesianus* from its type locality in Amazonas, Brazil. **Journal of Herpetology**, **37**(4):754-757.

NASCIMENTO, L.B.; LEITE, F. & WACHLEVSKI, M.,

2005. Anuros. In: SILVA, A.C.; PEDREIRA, L.C.V.S.F.; ABREU, P.A.A. (Orgs.) **Serra do Espinhaço Meridional: Paisagens e Ambientes**. Belo Horizonte: O Lutador. Cap. XII, p.209-230.

OWASKA, K. & RAND, A.S., 2001. Courtship and reproductive behavior of the frog *Eleutherodactylus diastema* (Anura: Leptodactylidae) in Gamboa, Panama. **Journal of Herpetology**, **35**(1):44-50.

PEDRALLI, G.; GUIMARÃES NETO, A.S. & TEIXEIRA, M.C.B., 2000. Diversidade de anfibios na região de Ouro Preto. **Ciência Hoje**, **30**(178):70-73.

POMBAL JR.; J.P.; SAZIMA, I. & HADDAD, C.F.B., 1994. Breeding behavior on the pumpkin toadlet, *Brachycephalus ephippium* (Brachycephalidae). **Journal of Herpetology**, **28**(4):516-519.

SALTHE, S.N., 1969. Reproductive modes and the number and sizes of ova in the urodeles. **American Midland Naturalist**, **81**(2):467-490.

SALTHE, S.N. & DUELLMAN, W.E., 1973. Quantitative constraints associated with reproductive mode in anurans. In: VIAL, J.R. (Ed.) **Evolutionary Biology of Anurans: Contemporary Research on Major Problems**. Columbia: University Missouri Press, p.229-249.

STATSOFT, Inc. 1995. **Statistica for Windows version 5.1**. Tulsa.

WELLS, K.D., 1977. The courtship of frogs. In: TAYLOR, D.H. & GUTTMAN, S.I. (Eds.) **The Reproductive Biology of Amphibians**. New York: Plenum Press. p.253-262.

WELLS, K.D., 1980. Social behavior and communication of a dendrobatid frog (*Colostethus trinitatis*). **Herpetologica**, **36**:189-199.